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Canopy transpiration of Jeffrey pine in mesic and xeric microsites: O_3 uptake and injury response

Abstract Canopy transpiration of mature Jeffrey pine was compared in "mesic" and "xeric" microsites differing in topographical position, bole growth, and the level of drought stress experienced. Diurnal and seasonal course of canopy transpiration was monitored with thermal dissipation probes in 1999 and 2000. Mid-canopy measures of diurnal foliar stomatal conductance (gs) were taken in June and August in 1999. In early summer, there was little difference between trees in either microsite with regard to gs (55 mmol H_2O m^{-2}s^{-1}), canopy transpiration (4.0 l h^{-1}), and total duration of active transpiration (12 h >0.03 l h^{-1}). In late summer, xeric trees had a lower daily maximum gs (by 30%), a greater reduction in whole canopy transpiration relative to the seasonal maximum (66 vs 79%), and stomata were open 2 h less per day than in mesic trees. Based on leaf-level gas exchange measurements, trees in mesic sites had an estimated 46% decrease in O_3 uptake from June to August. Xeric trees had an estimated 72% decrease over the same time period. A multivariate analysis of morphological and tissue chemistry attributes in mid-canopy elucidated differences in mesic and xeric tree response. Mesic trees exhibited more O_3 injury than xeric trees based on reduced foliar nitrogen content and needle retention in mid-canopy.

Keywords O_3 injury · Water relations · Stomatal conductance · Drought · Jeffrey pine

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Introduction

Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) is a widespread, economically important conifer in the western United States (Oliver and Ryker 1994). The species is sensitive to O_3 injury (Miller et al. 1983), and most trees exhibit some foliar injury on older needles in areas of moderate O_3 exposure. [In this paper, moderate O_3 exposure is defined as a cumulative, seasonal value of less than 250 ppm h^{-1}, based on 24 h, for the period April 15 through October 15.] Sequoia National Park experiences O_3 that is produced in San Francisco and the San Joaquin Valley and transported east to the Sierra Nevada (Unger 1978). Daily maximum O_3 concentrations exceed California state standards (95 ppb) on average 32 times per summer (Fig. 1), based on a 16 year database (1984–2000, National Park Service, Air Resource Division,
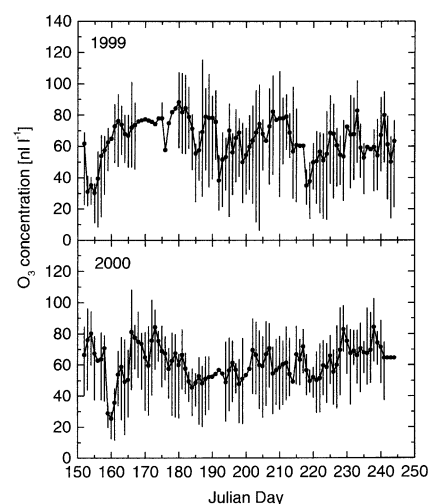

Fig. 1 Daily maxima, minima, and mean O_3 concentration (ppb) for the hours 0600 to 1800 in summer of 1999 and 2000. Data begin with June 1 and end with August 30, with day of year indicated on the *x*-axis. Symbols with only the daytime average indicate days for which >4 h of data were missing. Data courtesy of the Resource Management Office, Sequoia National Park, Calif.

Sequoia National Park-Lower Kaweah monitoring station, www2.nps.gov/ard/investhp.html).

Jeffrey pine occurs in a range of microsites within the mid-elevation, mixed conifer forests in the Sierra Nevada, from riparian margins, to mid-slope seeps and swales, to isolated individuals on rocky outcrops. We tested whether Jeffrey pine had differing transpirational patterns (diurnal, seasonal) in mesic (seeps, riparian margins) vs xeric (rocky outcrop) microsites. Were trees in rocky outcrops more drought-stressed than those in riparian margins, or had they gained reliable access to groundwater? Did drought stress translate to lower canopy transpiration? If trees in the two microsites had differing canopy transpiration and canopy O_3 uptake, did the level of O_3 injury also differ?

In the level II approach of the critical loads concept adopted by the UN-ECE, drought is considered a major factor modifying the O_3 effect on plants (Führer et al. 1997). Drought-induced stomatal closure limits pollution uptake and could protect plants from O_3 damage. However, drought itself may generate oxidative stress in the plant tissues (Smirnoff 1993; Pell et al. 1997). Ozone also affects plants through oxidative stress mechanisms (Polle 1998), and a synergistic interaction of O_3 exposure and drought is conceivable. We characterized the level of drought stress experienced, and used biological response attributes to help verify differences in O_3 effects on Jeffrey pine growing in mesic and xeric microsites.

Materials and methods

Field site

A Jeffrey pine stand on a south-facing slope at 2,170 m in Sequoia National Park was selected for study. The site was within 4 km of the village of Lodgepole, California. The vegetation type was pine-dominated, Sierran mixed conifer forest (sensu Barbour 1988).

Sampled trees

Mature Jeffrey pine trees were selected within an area approximately 3 km² based on a range in bole diameters (18–47 cm). The resulting sample of 130 trees averaged 32±7 cm in bole diameter, 17±5 m in height, and 104±36 years in age at 1.5 m (mean ± standard deviation). Trees were identified as mesic or xeric by topographical position in the landscape. Riparian trees (mesic) were by necessity all in one topographic position, but seep (mesic) and rocky outcrop (xeric) trees were intermingled across the slope. We measured morphological attributes in mid-canopy on 60 trees in 2000, seasonal canopy transpiration responses on 32 trees (16 in 1999, and 16 different trees in 2000), and leaf-level gas exchange at mid-canopy on 16 trees (1999). Each subset of trees was evenly divided between mesic and xeric microsites. We rejected whole canopy transpiration data on three trees because of mistletoe infection and extensive bark beetle damage.

The assignment of trees to the mesic or xeric microsite was assessed (verified) with an analysis of basal area increment in tree boles. Annual radial bole growth was measured (Peterson et al. 1991), annual percent increase in basal area increment (BAI) was calculated, and the BAI in average or above-average years was compared to that in below-average precipitation years. We tested the hypothesis that mesic trees had greater bole growth rates and,
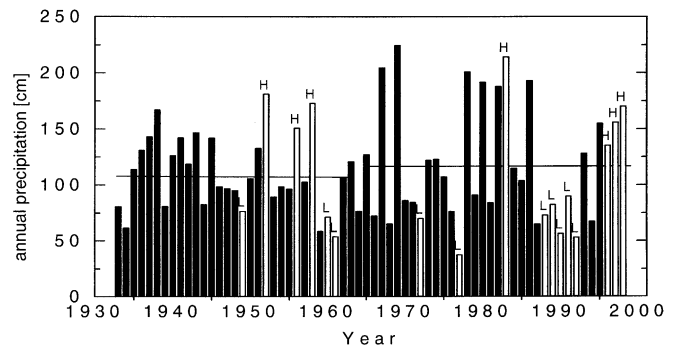

Fig. 2 Total annual precipitation (cm) in the mixed conifer forest, Sequoia National Park, from 1933 to 1998. The precipitation gauge was located in Giant Forest from 1932 to 1968 and in Lodgepole from 1968 on. *Horizontal lines* Average precipitation at each location. Data courtesy of the Resource Management Office, Sequoia National Park, Calif. *H* Years with ≥20% above average precipitation, *L* years with ≤20% below average precipitation

although possibly affected by multi-year drought, were responsive to above-average precipitation years.

A long-term record of precipitation exists for Giant Forest (1932–1968) and for Lodgepole (1969–2000), 6 km to the north (Fig. 2). Despite similar elevations, the average annual precipitation differed by 10 cm between the two sites, so above- and below-average precipitation years were defined as a percentage of the site average (>120%, <80%, respectively). Above-average precipitation years were chosen if preceded by an average or above year. The 1 year delay was imposed because not all trees in each of the two microsites responded in the first year to improved water availability. Both endogenous (within tree carbon allocation to bole growth in drought years combined with moderate ozone exposure) and environmental factors (temporal and spatial variability in groundwater recharge for that tree) possibly contribute to the delay in response of some trees. For all trees, the expected response occurred by the second year of above- or below-average precipitation. Bole wood production for the 16 trees in each microsite was tested with an ANOVA for 7 average- or above-average precipitation years and 10 below-average precipitation years.

Water relations

Needle xylem water potentials (ψ_L) were determined on previous year's fascicles at pre-dawn and solar noon with a pressure chamber (PMS, Corvallis, Ore.: Pallardy et al. 1991). Foliar water content of the same needles was also determined [(field weight − dry weight)/(dry weight)×100%].

Gas exchange measurements

In 1999, diurnal gas exchange was measured on three primary branches of 16 trees at the end of June (June 24 through July 2) and the end of August (August 18 through 27). No leaf-level gas exchange measurements were conducted in 2000. The mid-canopy was accessed by a 15 m tall, portable aluminum scaffolding (Genie, Portland, Ore.). Instantaneous gas exchange measures were conducted with both an open (Model 6400, LiCor Instruments, Lincoln, Neb.) and closed photosynthetic system (Model 6200; using a modified technique to optimize for measurement of water vapor exchange, Grulke et al. 2002). Stomatal conductance measured with the two instruments was similar at low values (within 3–4 mmol H_2O m^{-2} s^{-1}) and indistinguishable at values >20 mmol H_2O m^{-2} s^{-1}. Needle surface area (A) was calculated from measurements of fascicle diameter (D) and needle length (L) [A = (Dπ×L+3D×L)].

Ozone uptake was calculated from hourly O_3 data (National Park Service, www2.nps.gov/ard/investhp.html), average hourly gs for each tree based on leaf-level measurements, and a constant to accommodate the difference in diffusivity between water vapor and O_3 (Laisk et al. 1989).

Canopy transpiration

Trees were instrumented with Granier-type thermal dissipation (TD) probes (TDP-30, Dynamax, Houston, Texas) over two growing seasons (1999, 2000). Thermal dissipation probes were installed on the north side of the bole at 5 m, well below the first live branch. Because the trees twist as they grow, the canopy aspect represented by the exact location of the TD probe was unknown. In 1999, there were many missing data due to poor battery recharge from the solar panels, poor functioning of one of the data loggers (four trees), and repeated disturbance by wildlife (e.g., bears, woodpeckers, raccoons, fishers). In 2000, nearly continuous data were obtained from seven mesic and nine xeric trees.

Morphological and tissue chemistry attributes associated with O3 injury

Similar to the approach taken with a ponderosa pine O_3 injury assessment (Grulke and Lee 1997), we used a multivariate analysis of morphological and tissue chemistry attributes (divisive clustering analysis; S-Plus 2000) to differentiate tree response between the two microsites. Nine attributes were quantitatively determined to be correlated with O_3 injury in ponderosa pine (methods described in Grulke and Lee 1997). We measured the recommended attributes [2nd whorl chlorotic mottle, number of needle age classes retained, proportion of the branchlet foliated (length of branchlet foliated divided by the total branchlet length), branchlet diameter, % foliar nitrogen content, distance to nearest conspecific neighbor], and three others (4th whorl chlorotic mottle, specific leaf weight, foliar C:N) to assess biological response to O_3 uptake in this closely related species in August 2000. We omitted BAI, because it was used for the initial categorical assignment to mesic or xeric microsite. All foliar and branch attributes were measured on previous year tissue. The two most commonly used O_3 assessment methods for pine-dominated forests in the western United States were also applied to trees in the two microsites [ozone injury index (OII); forest pest management assessment (FPM); Miller et al. 1996]. Clustering analysis was performed on data collected at mid-canopy for 60 trees. Differences in attributes between microsites were tested with *t*-tests. All calculations were performed with S-Plus (2000).

Results

Basal area increment

The assignment of trees to the mesic or xeric microsite was validated by testing for differences in BAI between trees in the two microsites in years of above- and below-average precipitation. BAI was greater in mesic versus xeric site trees in both above- and below-average precipitation years. BAI of mesic trees responded significantly to above-average precipitation years, but xeric trees did not. The percent change in annual BAI of trees in mesic sites differed significantly ($P<0.001$) between above- and below-average precipitation years (3.02 ± 0.39 and 2.63 ± 0.41, respectively). The percent change in annual BAI of trees in xeric sites responded little between

Table 1 Summary water relations, maximum daily stomatal conductance (gs), and O_3 uptake on a single day in June and August (based on leaf-level measures of diurnal gs) of mesic and xeric trees. Needle xylem water potential is given in MPa; foliar moisture content is given in % of dry weight; gs is given in mmol H_2O m^{-2} s^{-1}. O_3 uptake is given in mmol m^{-2} day^{-1}. Values given are mean ± 1 SE. Lower case letters denote significance at the $P=0.05$ level

	June 1999	August 1999
Pre-dawn needle water potential		
Mesic	$-0.8\pm0.1a$	$-1.0\pm0.2a$
Xeric	$-1.1\pm0.1a$	$-0.9\pm0.2a$
Foliar moisture content, pre-dawn		
Mesic	$134\pm9a$	$120\pm7a$
Xeric	$132\pm11a$	$112\pm6c$
Maximum diurnal gs		
Mesic	$55.4\pm2.5a$	$46.7\pm5.1a$
Xeric	$55.5\pm3.4a$	$30.0\pm5.1b$
O_3 uptake		
Mesic	$20.15\pm1.52a$	$10.44\pm1.67c$
Xeric	$15.97\pm1.81b$	$4.25\pm0.79d$

above- and below-average precipitation years (1.38 ± 0.19 and 1.29 ± 0.17, respectively).

Leaf-level water relations and gas exchange measures

Pre-dawn needle xylem potential did not differ between microsites in either early or late summer (Table 1). Pre-dawn foliar moisture content differed significantly between the June and August measurements, as well as between trees in mesic and xeric microsites in August. In early summer, there were no differences in maximum daily gs between trees in the two microsites (mesic vs xeric: 55.4 ± 2.5 vs 55.5 ± 3.4 mmol H_2O m^{-2} s^{-1}) (Table 1). The diurnal patterns of gs measured at mid-canopy were also similar between mesic and xeric trees in early summer (Fig. 3). In late summer, the maximum daily gs was significantly lower for trees in xeric (30.0 ± 5.1 mmol H_2O m^{-2} s^{-1}) vs mesic microsites (46.7 ± 5.1 mmol H_2O m^{-2} s^{-1}) (Table 1). In late summer there was very limited gas exchange throughout the day for trees in xeric microsites (Fig. 3).

The differences in gs between the microsites translated to significant differences in O_3 uptake. In June, mesic trees had 20% greater O_3 uptake on a daily basis than xeric trees (20.15 ± 1.52 vs 15.97 ± 1.81 mmol O_3 m^{-2} day^{-1}), although hourly gs differed significantly only during 1 h (Fig. 3). In August, mesic trees had 60% higher O_3 uptake than xeric trees (10.44 ± 1.67 vs. 4.25 ± 0.79 mmol O_3 m^{-2} day^{-1}). Ozone uptake of mesic trees declined by 46% within the growing season, but uptake of xeric trees declined by 72%.
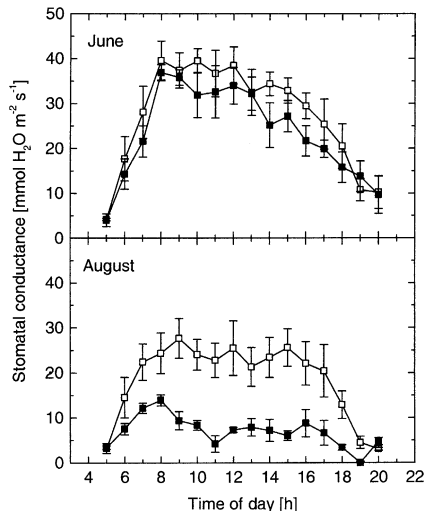
Fig. 3 Average diurnal stomatal conductance (gs, mmol H_2O m^{-2} s^{-1}) of Jeffrey pine trees in mesic (*open symbols*) and xeric (*closed symbols*) microsites at the end of June and at the end of August (mean values ±1 SD of *n*=8 trees for each microsite)
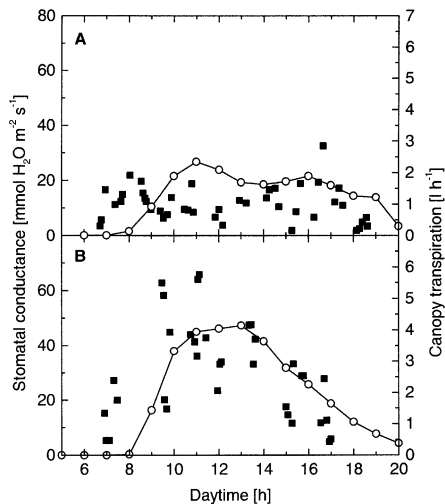

Fig. 4a, b Comparison of diurnal trends of leaf-level stomatal conductance (*filled squares*) in mid-canopy and whole canopy transpiration (*open circles*) for the same tree on the same day. **a** Xeric microsite, **b** mesic microsite

Comparison of diurnal patterns of leaf- and canopy-level gas exchange

Values of gs measured at mid-canopy via instantaneous gas exchange methods and canopy transpiration derived from TD probes had similar diurnal responses in both early and late summer (Fig. 4). For some of the trees instrumented, canopy transpiration began and ended when stomata opened and closed. For other trees, there was a temporal lag of up to 1.5 h between canopy transpiration and stomatal opening (not shown). Sources of these errors are discussed in Becker (1998), and Grime and Sinclair (1999). Canopy transpiration rates as derived from TD

probes were similar to those reported for ponderosa pine and Douglas fir (Lopushinsky 1986; Granier 1987).

Seasonal trends in canopy transpiration

The canopy transpiration of trees in mesic microsites appeared to have two seasonal patterns: (1) constant, high transpiration throughout the growing season; (2) high early summer transpiration with a gradual decline of transpiration beginning as early as mid-July to as late as the third week of August. Both seasonal patterns of canopy transpiration occurred in riparian margins and mid-slope seeps. Trees in xeric microsites had significant, abrupt declines in canopy transpiration between mid-June and late-July. Because there was a considerable range in the date of the onset of drought-induced decline in canopy transpiration, seasonal trends in canopy transpiration from partial seasonal data in 1999 could not be reconstructed. In 1999, three periods of 10 days each were used to test for differences in gs between microsites. In 2000, the data set was more complete and six periods were used (Fig. 5).

Because there was a 10-fold difference in total daily transpiration between trees within the same microsite, summary statistics were performed on the percent maximum total daily canopy transpiration (Fig. 5). In 2 weeks in June (days 152–166 in 2000), canopy transpiration of mesic and xeric microsite trees was similar, but highly variable due to a cloudy period. For the rest of the summer, there were significant differences between trees in the two microsites on most days. The application of this technique was semi-quantitative and its purpose was to determine within-season changes in canopy transpiration between the two microsites: O_3 uptake should not be calculated directly from these data. However, the seasonal patterns and microsite differences in canopy transpiration data corroborate leaf-level gas exchange measures, e.g., that O_3 uptake was lower for trees in xeric microsites.

Assessment of biological response to O_3 uptake in the two microsites

The two standard indices used to assess O_3 injury in yellow pines gave differing conclusions. According to the OII score, mesic trees were slightly more injured than xeric trees (38.4±2.9 vs 32.3±4.1). According to the FPM score, mesic trees were slightly less injured (2.5±0.3 vs 2.9±0.2). These scores are generally calculated only for lower canopy, but we also collected data and calculated scores for mid-canopy. In mid-canopy, the OII score still suggested greater injury in mesic trees (38.4±3.0 vs 35.7±3.6). The FPM score did not differ between mesic and xeric trees in mid-canopy (both 1.7±0.1).

Multivariate analysis was applied to the morphological and tissue chemistry of the 32 trees monitored for leaf- and canopy-level gas exchange. We tried agglomerative and divisive clustering, as well as fuzzy partitioning techniques (S-Plus 2000) with various combinations of
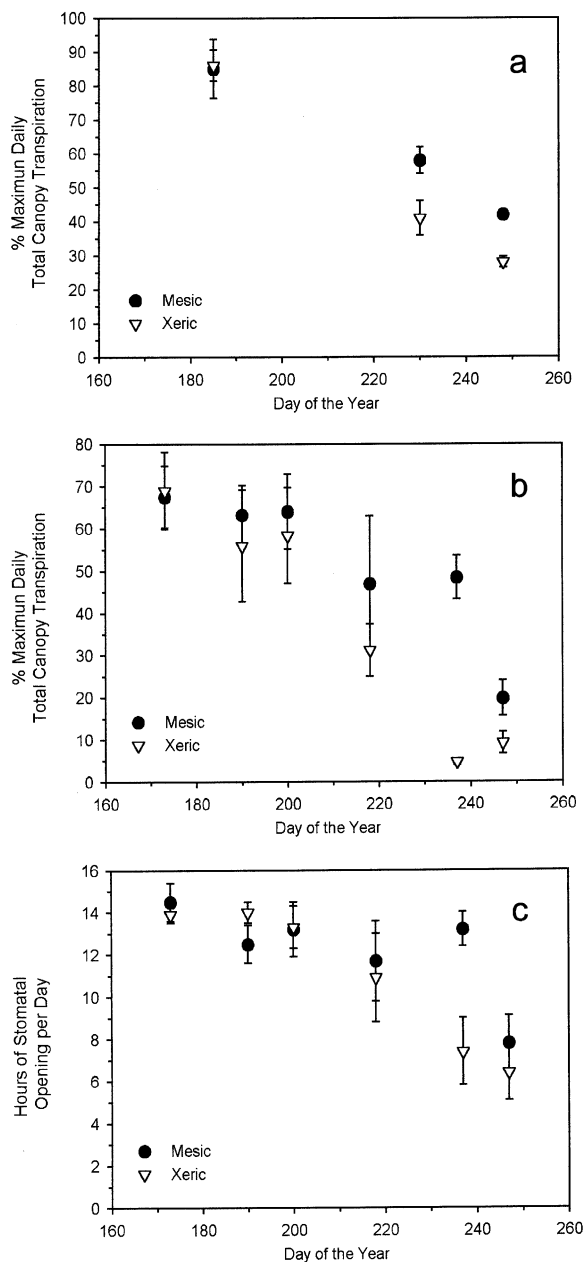
Fig. 5a–c Seasonal changes in canopy transpiration expressed as a percentage of the maximum. The symbols represent averages of 4–9 trees per microsite per sampling period (8–15 days each) of continuous data for **a** 1999 and **b** 2000. *Error bars* ±1 SD about the mean. **c** Average number of hours of stomatal opening for the same sampling periods for 2000

Fig. 6 Divisive cluster analysis of morphological and tissue chemistry attributes associated with oxidant injury for the 32 trees measured for leaf-level and whole canopy transpiration in 1999 and 2000

Table 2 Comparison of morphological and tissue chemistry attributes for 30 trees each in mesic and xeric microsites. Foliage or branch material from the previous year has been measured. Different letters denote significance at the $P=0.05$ level. Common O_3 injury scores (*OII* ozone injury index, *FPM* forest pest management) are also listed for the two microsites

Microsites	Mesic	Xeric
% Chlorotic mottle	2.8±0.3a	4.5±1.1b
% Foliar nitrogen	1.07±0.2a	1.13±0.2a
Foliar C:N	45.7±0.9a	42.5±0.8b
Specific leaf weight, cm^2 g^{-1}	36.6±0.7a	36.8±0.7a
Number of needle age classes	4.6±0.2a	4.9±0.2a
% Branch foliated	68±1a	73±2b
Branch diameter, mm	11.6±0.3a	12.4±0.4b
OII	38.4±2.9a	32.3±4.1a
FPM	2.5±0.3a	2.9±0.2a

the eight morphological and tissue chemistry attributes. Of these, the best separation was obtained with divisive clustering. Fuzzy partitioning assigned trees to the same groups. Chlorotic mottling of the fourth whorl did not aid in distinguishing Jeffrey pine response in the two microsites, and omitting conspecific nearest neighbor did not alter tree assignment to one group or the other. A new variable (specific leaf weight, suggested by Ewell et al. 1989) was added to the previous approach (Grulke and
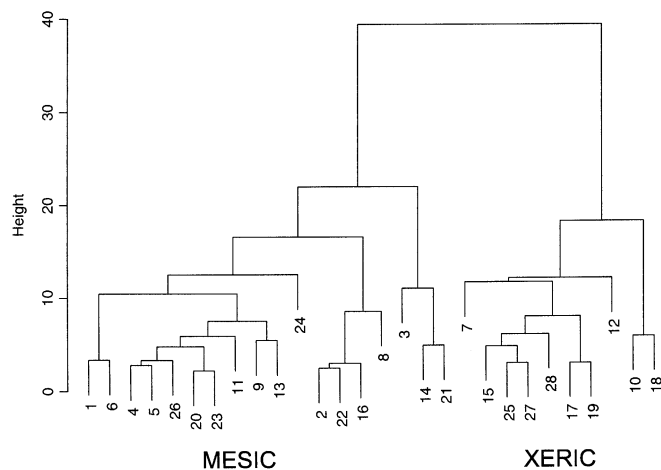
Lee 1997) and significantly aided separation of trees into two groups.

In the predominantly xeric tree group cluster, 30% of the mesic trees were included (Fig. 6). Of these, all were seep trees (e.g., no riparian trees were included in the xeric tree grouping). In the predominantly mesic tree cluster, 40% of the trees were misclassified. These results suggest that multivariate patterns of canopy attributes are related to microsite conditions.

We assessed the same attributes of a larger proportion of the population taken at mid-canopy to help interpret these results. The average values for components of morphological attributes in mid-canopy of 60 trees are summarized in Table 2. Mesic trees had lower chlorotic mottle in previous year needles, higher foliar C:N, lower within-whorl retention, and lower branchlet diameter. Although the number of needle age classes was slightly lower in mesic trees, the difference was not significant. From lower within-whorl retention, lower number of needle age classes retained, and lower branchlet diameter

in mid-canopy (the largest portion of canopy biomass occurs in the middle third of the canopy), we deduced that mesic trees exhibited more O_3 injury. We discounted lower chlorotic mottle in foliage of mesic trees because drought alone could have increased chlorotic mottle in xeric-site trees. We discounted lower foliar N concentration in mesic trees because this could be due to a dilution effect from greater needle elongation growth. Foliar carbon concentrations were nearly identical.

Discussion

Trees in xeric microsites may be using a deep groundwater source to maintain favorable water status through the growing season (Hubbert 1999; Dawson 1994), but this was apparently insufficient to prevent drought stress, as inferred by stomatal closure, in late August. Trees in xeric microsites had lower relative water content, and lower maximum daily gs relative to trees in mesic microsites in late August. Also, early and late summer diurnal patterns of gs were similar in mesic microsites, but in xeric microsites, gs was significantly depressed throughout the day in August relative to June measurements. Because mesic and xeric trees were largely intermingled, and O_3 exposure should be similar across the site, drought stress in xeric microsites should translate to lower O_3 uptake. By this reasoning, xeric trees should have had lower foliar O_3 injury. In contrast to expectations, Jeffrey pine from xeric microsites had greater chlorotic mottling of 2-year-old needles (Table 2).

Foliar chlorotic mottle has long been established as a definitive symptom of oxidant injury of yellow pine (i.e., ponderosa and Jeffrey pine; Miller et al. 1996). However, greater chlorotic mottling in xeric microsites may be indicative of other or multiple stressors (O_3 plus drought stress), and not just O_3 injury. When O_3 is taken up into the substomatal cavity, reactive oxygen species (ROS) are formed that directly injure cell membranes, and instigate a series of biochemical stress responses (Polle 1998; De Kok and Tausz 2001). However, ROS may also be produced in chloroplasts under conditions of drought (Smirnoff 1993). With drought stress, stomatal closure would lead to energy absorption in chloroplasts that would not be used in the dark reaction due to low substomatal concentrations of CO_2 (C_i). When C_i is low, the excited electrons from the photosystems pass to O_2, yielding ROS, a situation called photo-oxidative stress. ROS may elicit the same visible symptoms whether produced internally from photo-oxidative stress due to low C_i or from stomatal uptake of O_3. Our observations of increased foliar injury xeric trees may be field evidence of this phenomenon. Alternatively, O_3 uptake and drought stress combine to elicit greater oxidant foliar injury as a generalized stress response, or towards a greater sensitivity of xeric trees to O_3. Ponderosa pine has significant early senescence of foliage in drought years (Grulke and Balduman 1999).

There are a number of other morphological, physiological, and tissue chemistry attributes associated with O_3 exposure and chlorotic mottle in yellow pine (reviewed in Grulke and Lee 1997). The analysis of these canopy attributes suggested differences between the microsites attributable not only to O_3 exposure, but also to drought status. There are two commonly used field methods for the assessment of O_3 injury in yellow pine in the western United States. One is univariate (FPM, the score is based on the needle age class that first exhibits chlorotic mottling), and the other is multivariate (OII, where the score is largely based on the level of chlorotic mottling across all needle age classes and needle retention). The FPM score suggested that xeric trees had greater O_3 injury, and the OII score suggested that mesic trees had greater O_3 injury.

We used six attributes for this study of Jeffrey pine (chlorotic mottle, number of needle age classes, within-whorl needle retention, % foliar N, specific leaf weight, and branch diameter) as suggested by previous work with ponderosa pine (Grulke and Lee 1997). In the latter paper, multivariate patterns of these variables could be assigned to the level of O_3 damage. In the present study, two groups, roughly dominated by mesic (60%) or xeric (70%) trees were separated by cluster analysis. The tree assignment to a particular group was robust with respect to the multivariate technique used (divisive clustering, agglomerative clustering, or fuzzy partitioning). The resulting groups suggest that drought stress at least partly governs the expression of morphological and tissue chemistry attributes in the canopy.

Mesic trees had lower chlorotic mottling, but lower foliar retention and branch growth in mid-canopy, both well-known responses to O_3 exposure in yellow pine (Miller et al. 1996). Foliar loss in mid-canopy could have significant repercussions for the long-term carbon balance of the tree. To our knowledge, there are no allometric data published for Jeffrey pine (absent in Ter-Mikaelian and Korzukhin 1997). However, at a site with similar background O_3 exposure, mid-canopy biomass accounted for 60% of the whole canopy biomass of 40-year-old trees of ponderosa pine (Grulke and Balduman 1999). Lower BAI was strongly correlated with lower branch diameter in ponderosa pine (Grulke and Lee 1997), but in this study of Jeffrey pine, mesic trees had higher bole growth but lower branch diameter in mid canopy. Clearly a better understanding of mature tree biomass allocation in response to O_3 exposure and drought stress is needed.

A reduction in foliar retention at mid-canopy, a shift in C:N in foliage, and lower branch diameter is the best evidence we can provide for the potential deleterious effect of increased O_3 uptake in mesic trees. On the other hand, several symptoms presumably indicative of O_3 injury were more related to drought stress. From the present study, we cannot clearly corroborate a protective effect of drought from O_3 uptake. A more thorough assessment, including foliar antioxidant levels as a measure for defense capacity, will be conducted for a greater number of trees from this site.

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